Rev. Écol. Biol. Sol, 1981, **18** (1) : 77-90.

Fungus gnats (Diptera: Mycetophilidae / Sciaridae) and the role of mycophagy in soil: a review

BY

E. S. BINNS

Glasshouse Crops Research Institute, Littlehampton, Sussex, England

INTRODUCTION

While the cytogenetics of a few species of sciarid fungus gnats have been studied intensively (see e.g. STEFFAN, 1966), knowledge of their ecology is so sparse that accounts of their biology in soil (e.g. RAW, 1967) are illustrated only by reference to species of economic importance, particularly those infesting mushrooms. However, the habits of the latter are themselves obscure. Not least is the taxonomic problem of identifying individuals of the Mycetophilidae and Sciaridae which, in many studies (although they are now separable) are grouped together, as formerly (EDWARDS, 1925), in the same family (Mycetophilidae). Therefore, while there is a considerable, but fragmentary, literature on these insects, one difficulty, is knowing which taxon is referred to. However, (EDWARDS, 1925) recognised the Sciarinae as one of ten subfamilies of the Mycetophilidae distinguishable, in the adult, by their eyes, which are nearly or quite connected above the antennae by a narrow bridge, and by their wing-veination. The features distinguishing the sciarid larvae (Family Sciaridae) from those of other fungus gnats (Fam. Mycetophiloidea) have been discussed by PLACHTER (1979). In the present account, the family names will be used only where the author's identification restricts the observation to that family; otherwise the term « fungus gnat » will be employed, referring to both families together.

The major ecological problem is the precise resolution of the relationship between fungus gnats and fungi in the context of the processes of decay of leaf litter. Nearly all observations prove to be anecdotal and unquantified.

Reçu le 9-6-80.

In these circumstances, the specific diversity of the soil fauna of fungus gnats cannot be gauged. Present evidence suggests that Mycetophilidae live primarily in fungal sporophores whereas the Sciaridae live primarily in soil and only secondarily in fungal sporophores and wood. VAN DER DRIFT (1951 b), BAILLIOT (1975) and THIEDE (1977) all claimed that the density of Mycetophilidae in soil was much lower than that of the Sciaridae. If this is indicative of their respective importance, the information on sciarids of economic importance may, perhaps, be of some relevance.

Most records of the occurrence of Mycetophilidae are associated with fungi (EDWARDS, 1925; KÜHNELT, 1961) and, together with those of Sciaridae (TUOMIKOSKI, 1960), with rotten-wood. In the apparent absence of fungal sporophores in a locality, EDWARDS (1925), speculated that Mycetophilidae were either « saprophagous » (without definition) (e.g. *Zygomyia* spp.) or « living under leaves » (e.g. *Mycomyia maura* Walk.). Such collections, as with pest species (HUSSEY & GURNEY, 1968), usually restrict attention to certain easily-delineated habitats (e.g. the fungal sporophore (EDWARDS, 1925, cf. KENNEDY, 1974)), to the neglect of the mycelium, which has resulted in the absence, save by BRAUNS (1954), VAN DER DRIFT (1951 b) and HEALEY & RUSSELL-SMITH (1972), of specific identification of litter-dwelling fungus gnats. EDWARDS (1925) did not, therefore, recognise the litter-dwelling habit, except by exclusion. However, apart from the Sciaridae, BRAUNS (1954) described some members of the Mycetophilidae (EDWARDS' 1925 sub-families the Sciophilinae and Mycetophilinae) as living in the F (fermentation) layer of soils although the only Mycetophilid obtained in a year's continuous emergence-trapping was *Tetragoneura sylvatica* (Curt.) (RUSSELL-SMITH; personal communication), which is known to feed on small pieces of rotten wood (MADWAR, 1937).

I. — ABUNDANCE OF LARVAE AND ADULTS

A) Agricultural Soils.

Under agricultural conditions, fungus gnats constitute a major part of the insect population. Thus, SCHAERFFENBERG (1939) numbered larvae of Sciaridae as the second most abundant dipteran family, both in species and numbers, in soil samples taken from pastures between December and March. OLECHOWICZ (1970) using emergence traps, showed that Sciaridae were the most numerous of six dipteran families identified in meadows, forming *c.* 37 % of the total Diptera. Similarly, in two years of suction-trapping over cereals, fungus gnats were found to be the second and fourth most numerous dipteran group (POTTS & VICKERMAN, 1974). Also, BRASSE (1975), using pitfall-traps in cereal fields over two years, found the larvae of Sciaridae the fourth most numerous dipteran family but contrasted this position with their even higher numerical status claimed by HEYDEMANN (1953). Using adult emergence traps in a winter wheat-fallow sequence, JONES (1976 a, b) singled out Sciaridae as sufficiently common for special attention and caught a *Bradysia* sp. from spring to summer but not during the winter nor, if the stubble was burned, in the autumn (JONES, 1976 a). In two years out of four, when numbers were highest, the populations emerging from fallow-soil exceeded those from cropped soils (JONES, 1976 b).

Also, by trapping emergent adults, BAILLIOT (1975) found that Sciaridae constituted 75 % of the insects under *Agrostis* grassland, 88 % under heathers and *Ilex galii* and 33 % under a pioneer flora of lichens, *Festuca* and *Agrostis*. The dominant sciarid species in these habitats were *Plastosciara* sp. (70 %), *Leptosciara autumnalis* Winn, (41 %) and *Carynoptera tetrachaeta* Tuom. (85 %), respectively. Emergent Mycetophilidae constituted less than 1 % in each habitat. Sciarid populations appeared as distinct generations in *C. tetrachaeta*, *Bradysia bicolor* (Meig.) and *Sciara nobilis* (Winn.) (3 generations/year) and in *B. paupera* Tuom. (2 gens./year).

The sciarid population associated with maize monoculture was assessed, in two seasons, by means of emergence traps, following different manurial treatments by BRUNEL & DELEPORTE-BAILLIOT (1978). Totals of sciarid emergence from organic manure treatments were 4.1 and 3.5 times as numerous as from soil treated with pig manure slurry and inorganic manuring respectively. The proportion of sciarids in the total catch of arthropods was 85, 72.5 and 75 % respectively. The most numerous of the sciarid species identified were *Scaptosciara vivida* Winn. (33-50 %) followed by *Bradysia paupera* Tuom. = *B. moestula* Tuom. > *B. strigata* Staeg. > other species. HART (1911) described an experiment in which the pots containing *Sciara*-infested cucumbers in sand were provided with a cube of decayed horse-manure. About the latter the larvae were subsequently found and the plants remained uninjured.

B) **Litter.**

While EDWARDS (1974), in a review of soil macro-arthropods, dealt with sciarids in only a single line, studies of fungus gnat biology have been made in connection with litter decomposition in different soils. Thus, ZACHARIAE (1965) concluded that the only arthropods of economic importance in the deciduous forests of Central Europe are the larger diplopod species and, among the insects, larvae of the dipteran families Tipulidae, Bibionidae, Mycetophilidae (Sciophilinae) and Lycoriidae (Sciaridae). Similarly, BORNEBUSCH * (1930) listed larvae of Mycetophilidae as the first or second most numerous dipteran taxon in beeth litter in five out of eight locations and in two out of four locations under spruce *(Picea abies)*.

By emergence trapping in woods of beech *(Fagus sylvatica)*, ALTMÜLLER (1979) showed that, in 1973, sciarids were the dominant family in the annual catch (78 % of total) and, between the beginning of April and November, when they were exceeded only once by species of Cecidomyidae. The dominant species (*Corynoptera* spp., *Ctenosciara hyalipennis* Meig. and *Epidapus atomarius* Deeger) were univoltine, producing their imagos in May when the minimum abundance of larvae was recorded. Thus, between March and November 1972, larvae of sciarids were dominant in flotation samples and only between April and June (i.e. the period of adult emergence) was their total less than 50 % of the whole.

---

* BORNEBUSCH (1930) and BAL (1970; see over), appear to use the term Mycetophilidae to include both Mycetophilidae and Sciaridae.

Under spruce (*Picea* sp.), THIEDE (1977) found sciarids were the most numerous pterygote insects in emergence (photo-eclector) traps. The twenty most numerous species were listed and, among the dipterous fauna, this diversity was exceeded only by the Mycetophilidae but these were much less abundant. 1,000-2,600 sciarid emergences per m^2 were recorded. Sciarids dominated the biomass so that *Plastosciara setifera* Lichtblau constituted 6-7 % in 1971 and *Ctenosciara hyalipennis* (Meig.) and *C. thiedei* Lichtblau, respectively, 18-33 % and 7-8 % of the biomass in 1972 and 1973, only a small number of species dominating the biomass in each year.

HEALEY & RUSSELL-SMITH (1972), who extracted larvae from soil by flotation, found, over two years, that larvae of fungus gnats amounted to 11-12 % of the annual population of litter from a mull and a moder woodland soil in 1968 and between 23-58 % in 1969 when they constituted the major taxon. In terms of the amount of tissue consumed, BAL (1970) claimed that larvae of Mycetophilidae are the major agents of « Vermoderung » under red oak *(Quercus borealis)* but are relegated to second place by phthiracarid mites under Douglas fir *(Pseudotsuga menziesii)* (cf. JACOT, 1939, below). HEALEY & RUSSELL-SMITH (1972) stated that their comparisons of abundance of fly larvae in mull and moder soils were distorted by the very high numbers of a *Sciara* sp. in the moder for a few weeks in the autumn of 1969 which were not noted the previous year. They also suggested that wide annual fluctuations (cf. THIEDE, 1977) are a feature of most of the more abundant groups of larvae Diptera in soils, although, in view of the probably of sampling errors, due to the clumped distributions recorded by VAN DER DRIFT (1951 b), such suggestions may be viewed with doubt (cf. KING, 1939).

RUSSELL-SMITH (1979) showed that, overall, adult Mycetophilidae had two peaks of activity (cf. SAKHAROVA, 1977) : in Spring, when a wood-inhabiting species was co-dominant with a species of unknown habitat, and in Autumn, when species of *Mycetophila*, known to intest agaric sporophores, were dominant. VAN DER DRIFT (1951 a) reported that visual searching of leaf-litter (which revealed an absence of larvae of Lycoriidae (= Sciaridae) in a calcareous mull throught the year), showed that the highest populations occurred during the winter on both an acid mull and a mor soil (although this technique probably revealed *c.* 5 % only of the total population (RUSSELL-SMITH, A. personal communication)).

However, ALTMÜLLER (1979) stated that the feeding of dipterous larvae was highest in autumn and winter when 76 % of the total energy turnover of the year 1972/73 was assimilated. In September, the first instar sciarids emerge achieving the maximum annual abundance of Diptera.

ZACHARIAE (1965) noted that the last autumn generation is still active under snow of frozen litter (cf. KÜHNELT, 1961). On the other hand, enough summer rain is necessary to maintain development (ZACHARIAE, 1965). Thus, JONES (1976 a) noted that, in one year out of eight, emergent adults of a *Bradysia* sp. were most common after a damp June. ZACHARIAE (1965) stated that fungus gnats of the above families pupate in response to drying of their substrate, though this has not been confirmed in *Lycoriella auripila* Winn. (BINNS, unpublished observation). However, BRAUNS (1954) noted that the Sciaridae, Sciophilidae and Fungivoridae have a strong affinity for moisture.

The growth efficiencies of young dipterous larvae were much higher than those of old larvae. Oxygen uptake was especially high in young instars but, on average, less than one third of larvae reached maturity (ALTMÜLLER, 1979).

II. — ROLE IN LEAF BREAKDOWN

A) Primary Decomposition.

EDWARDS (1974) compared sciarid larvae with those of bibionids in feeding, without preference, on both slightly- as well well-decayed leaves. Similarly, BRAUNS (1954) stated they occurred in both the F and H (= humus) layers of woodland. ALTMÜLLER (1979) noted that sciarid larvae consume not only the thin « shade leaves » but the thick « sun-leaves » as also did, particularly, the Sciophilidae. HEALEY & RUSSELL-SMITH (1972) showed that the soil population of sciarids, consisted of a single, dominant species; *Sciara* c.f. *autumnalis*, [= *Ctenosciara hyalipennis* (TUOMIKOSKI, 1960)]. This was abundant in the mull soil, under oak *(A. petraea)* with ash *(Fraxinus excelsior)* and birch *(Betula pendula)*, but was found almost entirely in the *humus layers*. However, in moder soil, under beech *(Fagus sylvatica)*, in the *(drier)* year of greatest abundance (cf. KING, 1939), when sciarids accounted for over half of thel mean annual soil population, *c.* 15 % of them were found in the *litter* layer. While the role of the soil fauna has been emphasised, the nature of the parent litter greatly influences its rate of breakdown by fungus gnats as well as other organisms. Thus, leaves of elm *(Ulmus procera)* are more readily attacked than those of oak, beech and coniferous trees which have a thick cuticle and cell walls (VAN DER DRIFT, 1951 a).

TWINN (1974), who studied oak mor, found little removal of particulate material during a period of *c.* 70 days after leaf-fall, as have other authors. However, a loss of *c.* 20 % in the dry weight of the leaf occurred during this period, due to the activities both of the microflora and the effects of leaching. Later the colonisation of the leaf-litter by the larger invertebrates, e.g. enchytraeids and fungus gnats, began.

BAL (1970) observed that larvae of Mycetophilidae developed rapidly on material from the F_1 layer but that they refused material from the litter layers and consequently died. It was suggested that the removal of certain metabolites (e.g. tannins) is essential. Alternative explanations might involve the softening and weakening of fallen leaves or the addition of feeding stimulants e.g. fungal hyphae (see below).

The action of micro-organisms greatly weakens the leaves of deciduous spp. and begins their fragmentation so rendering them suitable to the « primary devourers » (KÜHNELT, 1961). Holes are eaten in the leaf by sciarids (BRAUNS, 1954) but, at first, the veins are eaten more slowly and the mid-ribs not at all so the leaves are skeletonised to a varying degree. Fir-needles, however, are consumed only by biting off small particles and are mined only occasionally, particularly by the smaller instars (BAL, 1970). However, JACOT (1939) stated that larval sciarids are less common than the phthiracarid mites in fir litter and are usually found in needles which show more fungal decay. The larva is often found in a leaf with one or two saprophagous mites or their faeces. It is not certain if the egg is deposited in leaves containing mite faeces on which the larva then feeds, or whether the larva feeds on undisturbed tissue. From needles taken in late July, full-grown larvae and pupae were obtained together with leaves from which the adult fly had already emerged. The leaves in which these larvae were found were much more decayed, flaccid and paler, than those which harboured the mites. By adult emergence the leaves are much more decomposed than are those on which the mites mature. Thus, there is reason to believe that the larvae feed on mite faeces, further reducing them to a fine granular substance which would be much more easily washed into the soil by percolating rainwater.

B) **Feeding and excretion.**

According to ZACHARIAE (1951) the smaller, younger stages feed first on bacterial slime and fungal hyphae on the leaf-surface and then on the softened cell-layers of the lower epidermis of the leaf. BRAUNS (1954) figures Sciaridae as browsers on leaf surfaces infected with fungi. HEALEY & RUSSELL-SMITH (1972) found that their gut contents included a large proportion of plant cells (including epidermis and stomata), spores, pollen grains and fine humic particles. They also confirmed and extended information on the presence of fungal hyphae in *Lycoria* sp. previously noted by DUNGER (1963). Thus, on moder soils, a high proportion of basidiomycete hyphae was present which was not observed from samples taken from the mull soil. Conversely, those from the mull soil contained more mineral particles, which was probably due to the greater degree of mixing which these soils receive. BINNS (1980) stained the intestines of larvae of *Lycoriella auripila* Winn. from mushroom casing and found them to contain both peat and fungal material.

The tissue pattern of bitten-off pieces of oak leaf was said to be retained during passage through the gut (BAL, 1970). However, portions of fir needles, which can be consumed only by systematic biting-off, were smaller and retained practically no tissue structure.

During its passage through the intestines, ingested material becomes aggregated by mucus, and is voided as characteristic globules (BAL, 1970). In the oak and fir moder humus-profiles (BAL, 1970), the larvae were chiefly found on the underside of the F_1 horizon from which they scarcely moved. As a result, excrement accumulates in the upper part of the F_2 horizon (cf. VAN DER DRIFT, 1951 a) where, under the action of microbes and percolating rainfall, they form a greasy mass (BALL, 1970; ZACHARIAE, 1965). During this process excrements are strongly attacked by moulds so that they disintegrate completely. By contrast, excrements in the F_2 layer of a Douglas fir humus-profile retained their individual character much longer (BAL, 1970).

POBOZSNY (1976) recorded a narrowing of the carbon : nitrogen (C : N) ratio of leaf material consumed by larvae of *Bradysia brunnipes* Meig., such as occurs during the « humification » of soil organic matter (EDWARDS, 1974). POBOZSNY (1976) also showed that the main constituents removed by this sciarid were lignins, cellulose and fats; most animals lacking the capacity to digest the former two materials (KÜHNELT, 1961). DUNGER (1963) suspected that the action of symbiotic gut-bacteria accomplished the decomposition of cellulose in dipterous larvae. While ZACHARIAE (1965) concurred with this view, he emphasised the overriding role of the soil microflora (cf. CROSSLEY, 1977). Similarly, BURGES (1967) considered that the decomposition of lignin chiefly by the action of microbial enzymes. Thus, the prevailing view (see e.g. NEF, 1957) is that most chemical degradation of litter components is effected by fungi and bacteria, while the feeding activities of small invertebrates serve only to reduce the substrate to fragments of small size. However, MARTIN (1979) stated it seems possible that litter-feeding invertebrates might augment their digestive capabilites through the acquisition of fungal enzymes, and that significant digestion of plant cell-wall components might occur in the guts of litter-feeding arthropods.

On the other hand, sugar, starch, protein, pectin and hemicellulose contents were increased by passage through the intestine (POBOZSNY, 1976) and clearly provided an enriched food-supply for other soil organisms. ZACHARIAE (1965, cf. BURGES, 1967) identified these as enchytraeid worms, which feed upon the faeces of sciarids, together with other « microfloral grazers ». BINNS (unpublished observation) found that enchytraeids colonised mushroom compost some time after the larvae of sciarids, when its consistency was sticky and moist and unsuited for mycelial colonisation (HUSSEY & GURNEY, 1968).

C) **Populations.**

ZACHARIAE (1965) considered the larvae of Lycoriidae, Mycetophilidae (Sciophilidae) and Fungivoridae to be gregarious. TUOMIKOSKI (1957) noted little tendency on the part of bark-dwelling sciarids to migrate from the natal egg-mass. Relatively little movement was recorded by BAL (1970) who considered the larvae of Mycetophilidae to be « sessile ». As a result, they may undertake relatively little *transportation* or mixing of soil material or *inoculation* of microorganisms (cf. VAN DER DRIFT, 1951 a). Thus, PHERSON & BEATTLE (1979), in a study of this habitat, considered only the dispersive role of the fungal-loads of acarines, collembola and diplopods.

LLOYD (1963) observed animals living under the loose bark of fallen beech branches to test whether mass movements into litter occur during severe weather. However, populations of sciarids in bark and litter appeared to be independant. KING (1939) noted that slow movement within the soil renders the flexibility of food habits (cf. EDWARDS, 1974); above) of great significance for species or stages confined there, facultative saprophytes having an advantage over strictly phytophagous forms.

VAN DER DRIFT (1951 b) found groups of young larvae of *Lycoria sociata Win.* regularly dispersed through beech woods. The number of larvae in a group ranged from hundreds to some thousands, their wholesale appearance being reminiscent of army-worms, though no migration was observed. Such large numbers did cause the *removal* of the lower litter layers; over a larger area than that occupied by the larvae, indicating some horizontal movement. Sciarids were, therefore, considered to constitute a major component of litter breakdown which opinion, on account of their abundance, was held by

BORNEBUSCH (1930). On the basis of measurements of the standard deviation of populations trapped, THIEDE (1977) also concluded that the majority of sciarid species had a discontinuous distribution.

On the basis of equivalence with the energy consumption of millipedes, ALTMÜLLER (1979) considered that Sciaridae and Sciophilidae consumed 13.5-29 % of the annual leaf fall in 1972/73. They produced 203-436 kcal × 10^4/ha/year faeces and were considered to constitute an important factor in breaking down dead leaves of beech (ALTMÜLLER, 1979). The total assimilation was about 40 kcal/m^4/year in 1972/73. This is approximately 0.1 % of the net primary production of the green plants especially *Fagus sylvatica*. However, little attention has been paid to the role of fungus gnats in the last of VAN DER DRIFT's (1951 a) functions of the feeding dipterous larvae, i.e. of « *sanitation* » and the effect of fungal grazing on colonisation by fungi (see below).

III. — RELATIONS WITH FUNGI AND PLANTS

A) Saprophagy.

STEFFAN (1966) stated that sciarid larvae generally feed upon decaying plant material (phyto-saprophagous), animal excrement (coprophagous), and fungi (mycetophagous). However, as fungi are intimately associated with decay and excrement, these categories can doubtfully be exclusive. Thus, the largest group of larvae examined by STEFFAN (1974) was said to be phyto-saprophagous and/or mycetophagous. KENNEDY (1974), who distinguished those sciarid spp. which fed upon decaying roots and stems from those which feed on *apparently* healthy tissue (Conclusions), suggested that sciarid larvae may utilise fungi as a primary food source instead of the substrate on which they occur (cf. BAUMBERGER, 1919). The substrate itself may pass through the insect relatively unchanged (MINDERMAN & DANIELS, 1967).

Relatively little information is available concerning the role of insects and their interaction with the succession of fungal invaders of their substrate. Their status as (phytophagous) pests of plants is, correspondingly, unclear.

B) Phytophagy.

LEITH & NEWTON (1969) found that sciarid larvae sometimes fed on stem and leaf-tissue as well as on roots. Similarly, HUSSEY (1964) found *Bradysia paupera* feeding on the leaves of apparently healthy cucumbers. VAN DER DRIFT (1951 a) noted, however, that, by exposing the plant tissues, the feeding process itself creates an entry for attack by microorganisms. Thus, LEATH & NEWTON (1969) also showed that plant deaths due to *Fusarium* spp. were greater in the presence of larvae of *Bradysia*. Larvae have, therefore, shown a propensity to attack healthy plants, together with an ability to introduce disease organisms. The prevalence of this latter habit is not known. It appears that sciarid root-feeders can, at times, behave in such a way as to increase the supply of litter to the soil (BINNS, 1977).

The activities of sciarids in litter appear to proceed at a correspondingly early stage of soil-formation. This is suggested by the observation of BRAUNS (1974) on leaf holing and HEALEY & RUSSELL-SMITH (1972) on the presence of larvae in the litter layers (e.g. *Phytosciara (Phorodonta) flavipes* Meig. — though not a numerous species) and underlies many of the observations of BAL (1970).

C) **Mycophagy.**

RAW (1967) noted mycetophilids as fungal feeders. Studies on the sciarid pests of mushrooms suggest an antagonism between the colonisation of compost by mycelium or by sciarids. Compost well-colonised by mycelium was unattractive to ovipositing *Lycoriella auripila* Winn. save for a period of little more than their generation-time (HUSSEY & GURNEY, 1968; Table 3). Infestation was renewed, however, after « casing » of the beds with peat and chalk, the application of which induced fruiting. Sciarid larvae could be reared to maturity on detached (i.e. decomposing mushroom sporophores (BINNS, 1980)) and larvae may tunnel growing mushrooms (though this is of little economic significance (HUSSEY & GURNEY, 1968)). Out of doors, TRIFOURKIS (1977) stated that sciarid colonisation of mushroom sporophores occurred at an early stage of decomposition and larvae fed on sporophore tissue (BINNS, 1980). Thus, while sciarid development may occur, both on the uncolonised substrate (i.e. unspawned compost) and on the decomposing mushroom, it is correspondingly favoured by the intermediate stage of *colonisation* of the compost by the growing mycelium (BINNS, 1975, 1980).

In fact, experiments showed that larval development of *L. auripila* was more rapid on compost partially colonized by mycelium than on compost free from all mycelium (BINNS, 1975). Though comparisons can be misleading, more larvae of the American mushroom pest species *L. mali* (Fitch) *(Sciara pauciseta)* also develop on spawned rather than sterilized compost, the former being more attractive to both larvae and adults (MACDONALD, 1972). Again, early observations at the GCRI (HUSSEY, 1956) showed that more adult *L. auripila* emerged from spawned than from unspawned compost exposed in the open.

In the case of *Sciara coprophila*, mycelium was eaten and the compost rejected (THOMAS, in LUTZ *et al.*, 1937). Similarly, ELLISOR (1934) stated that the development of the plant pest *Neosciara ocellaris* (Comstack) was more rapid on decomposing than on fresh food. In laboratory experiments with another sciarid plant pest, *Bradysia impatiens* (Johanssen), KENNEDY (1974) showed that mean survival time was higher and mean developmental time lower when larvae were allowed access to a fungus (*Alternaria tenuis* Auct.) growing on a lima bean agar substrate than when feeding on the substrate alone.

D) **Mycelium ageing and migration.**

Complete fugal colonisation curtails the activities of the sciarid, for HUSSEY & GURNEY (1968) found that fewer second generation adult sciarids emerged after females were exposed to successively older samples of compost, measured from the date of spawning. This may be related to the ageing of the mycelium which is attended by a reduction in the rate of respiration but also of protein synthesis (Molitorius, Van Etten & Gottlieb, 1968); the major nutritional role of the mycelium being, for sciarids, as a nitrogen source (Binns, 1980).

Martin (1979) listed numerous classes of secondary fungal metabolites which are potentially harmful to mycophagous insects, as are the polysaccaride~~s~~ fungal cell-walls. Thus, calcium oxalate is known to be excreted during the growth of fungal mycelium (Latché & Piquemal, 1975). Addition of calcium oxalate impeded the development of sciarid larvae in compost (Binns, 1980) and probably limits mycelial feeding by sciarid larvae and provokes subsequent migration.

IV. — **CONCLUSIONS**

Although they recognised that the argument might appear to have been stated in reverse, the lack of a conception of the soil as an *ecological community* was suggested (Birch & Clark, 1953) as responsible for the scarcity of information on the relative roles on different organisms in plant litter decomposition.

No information is available on the interaction between the larvae of fungus gnats and fungal succession in litter. Saito (1966) found masses of faeces under the hymenomycete-infested leaves in the litter-layer under beech *(Fagus cremata)*. The litter-feeding animals showed a marked preference for leaves infected with litter-(i.e. lignin-) decomposing white-rotting hymenomycetes, in contrast to those of the alternative, non-lignin decomposing fungi of the brown-rot process. In laboratory tests, a larval scatopsid (Diptera : Scatopsidae) readily fed on mouldy leaves while brown and greyish-brown leaves remained intact. This study is of interest, not only as an experimental study of the role of the fungal succession on the infestation of litter, for experiments with mushroom compost showed that *Scatopse fuscipes* Meigen occupied a later position in the animal succession than did sciarid larvae (Binnss, 1973). More precise information on the place of sciarid larvae, so far appears to be lacking.

Thus, it is not known to what extent « sanitation » (browsing on fungi — as seems to be the habit of sciarids) controls or regulates (Crossley, 1977) fungal development and facilitates attack by successive organisms (Van der Drift, 1951 a). Minderman & Daniels (1967) considered the microflora that develops on newly-fallen leaves to be the most important source of nutrition (mainly easily digestable protein) for litter eaters [e.g. mycelial browsers such as sciarids (Brauns, 1954) see below], whereas the leaf-tissue acts as a substratum which is taken up only incidentally. It would also seem that, while sciarids are primarily mycophagous (cf. Binns, 1980), the existence of a microflora of the living leaf and root makes it difficult to distinguish the food source of the pest species (Kennedy, 1974). Similarly, the possible role of a symbiotic gut flora has yet to be studied.

However, while sciarid larvae may *appear* to be rather general feeders on litter, humus and fungal materials (HEALEY & RUSSELL-SMITH, 1972; EDWARDS, 1974), such a role is belied by the fluctuations of population which, the former authors stated, were especially marked in the fungus gnats. These species, they considered, were « opportunist » forms able, subject to climatic influence, to exploit short-term changes in the abundance of litter, fungal flora and other potential food supplies, in contrast to the model of stability suggested by the discussion of BURGES (1967; cf. KING, 1939). Similarly, THIEDE (1977) noted that the differences in the composition of arthropod numbers were more prominent between different years than between the different spruce stands studied in the same year. Such adaptations encourage the view that sciarids are *migrant* species (BINNS, 1979, 1980). One attribute of these is their rapid development, which enables them to respond to short-term changes (SOUTHWOOD, MAY, HASSELL & CONWAY, 1974). Thus, both BAL (1970) and ZACHARIAE (1965) concluded that fungal gnat larvae were rapidly maturing; presumably in comparison with the rest of the soil fauna (cf. BORNEBUSCH, 1930).

However, while MARTIN (1979) stated that « mycophagy is not simply a modification of phytophagy, but rather a feeding strategy which requires its own peculiar set of digestive and metabolic capacities », sciarid larvae, in particular, appear to maintain the capacity for both processes in large measure (BINNS, 1980) and are, therefore, well adapted as « primary devourers » (KÜHNELT, 1961) of litter which appears to be their special role (ALTMÜLLER, 1979). However, the basis of their association with plant material, either live or decaying, appears to be with fungal mycelium, the transient development of which, requires migration as an attribute of its exploiters (BINNS, 1979 ; 1980). The absence of males of certain sciarid species, from the trappings of THIEDE (1977), confirms that this is the major role of the sciarid female (BINNS, 1979).

ACKNOWLEDGEMENT

The author is grateful to A. RUSSELL-SMITH for helpful criticism, sources of reference and discussion of the manuscript.

SUMMARY

The abundance of soil-dwelling fungus-gnats and their role in the primary decomposition of litter is examined and the nature of their mycophagy is discussed. Sciarid fungus-gnats are adapted to exploit fungal growth associated with litter but this unstable resource requires that they are migratory.

RÉSUMÉ

L'abondance de sciarides mycétophiles dans le sol et leur importance dans la décomposition primaire de la litière ont été examinées ainsi que le mode de leur mycophagie. Les sciarides mycétophiles se sont adaptés à se nourrir de champignons se développant rapidement sur la litière tombée au sol mais cette ressource instable exige qu'ils soient migrateurs.

BIBLIOGRAPHY

ALTMÜLLER (R.), 1979. — Untersuchungen über den Energieumsatz von Dipterenpopulationen im Buchenwald (Luzulo-Fagetum). *Pedobiologia,* **19**: 145-278.

BAILLIOT (S.), 1975. — Études des mécanismes éco-éthologique de l'émergence chez quelques diptères chironomide et sciaride des landes armoricaines. Thèse de Troisième Cycle, Université de Rennes, 94 p.

BAL (L.), 1970. — Morphological investigation in two moder-humus profiles and the role of the soil fauna in their genesis. *Geoderma,* **4**: 5-36.

BAUMBERGER (J. P.), 1919. — A nutritional study of insects with special reference to micro-organisms and their substrata. *J. exp. Zool.,* **28**: 1-81.

BINNS (E. S.), 1973. — *Digamasellus fallax* (Leitner) phoretic on mushroom sciarid flies. *Acarologia,* **15**: 10-17.

BINNS (E. S.), 1975. — Mushroom mycelium and compost substrates in relation to the survival of the larvae of the sciarid *Lycoriella auripila. Ann. appl. Biol.,* **80**: 1-15.

BINNS (E. S.), 1977. — Fungus gnats. *The garden : Jl. R. hort. Soc.,* **102**: 76-78.

BINNS (E. S.), 1979. — Biology and behaviour of sciarid fungus gnats (Diptera : Sciaridae) in relation to swarming and migration. *Entomologist's mon. Mag.,* **115**: 77-90.

BINNS (E. S.), 1980. — Field and laboratory observations on the substrates of the mushroom fungus gnat *Lycoriella auripila* (Diptera : Sciaridal). *Ann. appl. Biol.,* **96**: 143-152.

BIRCH (L. C.) & CLARK (D. P.), 1953. — Forest soil as an ecological community. *Q. Rev. Biol.,* **18**: 13-36.

BORNEBUSCH (C. H.), 1930. — The fauna of forest soil. *Forst. ForsVaes. Dann.,* **11**: 1-158.

BRASSE (D.), 1975. — Die Arthropoden fauna von Getreidefeldern auf verschiedenen Böden im Brauschweiger Raum. *Pedobiologia,* **15**: 405-15.

BRAUNS (A.), 1954. — Terricole Dipterenlarven « *Musterschmidt* » Wissenschaftlicher Verlg, Göttingen, Frankfurt, Berlin.

BRUNEL (E.) & DELEPORTE-BAILLIOT (S.), 1978. — Influence de l'apport de différentes fumures sur la production des diptères en zone non bocagère dans une parcelle conduite en monoculture de maïs. Unpublished manuscript.

BURGES (A.), 1967. — The decomposition of organic matter in the soil. In : Burges (A.) & Raw (F.), eds. « Soil Biology », *Academic Press,* London, 479-492.

CROSSLEY (D. A. Jr.), 1977. — The roles of terrestrial saprophagous arthropods in forest soils : current status of concepts. In : « The Role of Arthropods in Forest Ecosystems », ed. Mattson (W. J.), *Springer-Verlag* : New York, 49-56.

DRIFT (J. van der), 1951 a. — The effects of animal activity in the litter layer. In : « Experimental pedology », eds. Hallsworth (E. G.) & Crawford (D. V.), *Butterworth,* London, 227-235.

DRIFT (J. van der), 1951 b. — Analysis of the animal community in a beech forest floor. *Tijdschr. Ent.,* **94**: 1-168.

DRIFT (J. van der), 1963. — The disappearance of litter in mull and mor in connection with weather conditions and the activity of the macrofauna. In : « Soil organism », eds. Doeksen (J.) and Drift (J. van der), *North-Holland Publishing Co.,* Amsterdam, 125-133.

DUNGER (W.), 1963. — Leistunsspezifität bei Streuzersetzern. In : Doekson (J.) & Drift (J. van der), eds. Soil organisms, *Nort-Holland Publishing Co.*, Amsterdam, 92-102.

EDWARDS (C. A.), 1974. — Macroathropods. Ch. 16 in : « Biology of plant litter decomposition ». Ed. Dickinson (C. H.) & Pugh (G. J. F.), Vol. 2, *Academic Press*, London, 533-554.

EDWARDS (F. W.), 1925. — British fungus-gnats (Diptera : Mycetophilidae), with a revised classification of the family. *Trans. R. ent. Soc. Lond.*, **1924**: 505-662.

ELLISOR (L. O.), 1934. — Notes on the biology and control of *Neosciara ocellaris* (Comstock) (Diptera : Sciaridae). *Iowa St. Coll. J. Sci.*, **9**: 25-36.

HART (C. A.), 1911. — Sciara notes taken by Mr Green. *26th Rept. of State entomologist Ill.*, 95-98.

HEALEY (I. N.) & RUSSELL-SMITH (A.), 1972. — Abundance and feeding preferences of fly larvae in two woodland soils. *Proc. 4th Int. Congr. Soil Zoology Dijon*, **1970**: 178-191.

HEYDEMANN (B.), 1953. — Agrarökologisch Problematik (dargetan an Untersuchungen über di Tierwelt der Bodenoberfläche der Kulturfelder). Diss. Univ. Kiel.

HUSSEY (N. W.), 1964. — Damage by larvae of *Hemineurina modesta. Pl. Pathology*, **13**: 138.

HUSSEY (N. W.) & GURNEY (B.), 1968. — Biology and control of the sciarid *Lycoriella auripila* Winn (Diptera : Lycoriidae) in mushroom culture. *Ann. appl. Biol.*, **62**: 395-403.

JACOT (A. P.), 1939. — Reduction of spruce and fir litter by minute animals. *J. For.*, **37**: 858-860.

JONES (M. G.), 1976 a. — The arthropod fauna of a winter wheat field. *J. appl. Ecol.*, **13**: 61-85.

JONES (M. G.), 1976 b. — Arthropods from fallow land in a winter wheat-fallow sequence. *J. appl. Ecol.*, **13**: 87-101.

KENNEDY (M. K.), 1974. — Survival and development of *Bradysia impatiens* (Diptera : Sciaridae) on fungal and non-fungal food sources. *Ann. ent. Soc. Am.*, **67**: 745-748.

KING (K. M.), 1939. — Population studies of soil insects. *Ecol. monogr.*, **9**: 270-286.

KÜHNELT (W.), 1961. — « Soil biology with special reference to the animal kingdom », *Faber & Faber*, London.

LATCHÉ (J.-C.) & PIQUEMAL (M.), 1975. — Variations des teneurs en acides aminés, amides et acides organiques dans les composts de culture d'*Agaricus bisporus* Lge., en fonction de la production de carpopores. *Annales Agronomiques*, **26**: 119-213.

LEATH (K. C.) & NEWTON (R. C.), 1969. — Interaction of a fungus gnat, *Bradysia* sp. (Sciaridae) with *Fusarium* spp. on alfalfa and red clover. *Phytopathology*, **59**: 257-258.

LLOYD (M.), 1963. — Numerical observations on movements of animals between beech litter and fallen branches. *J. Anim. Ecol.*, **32**: 157-163.

LUTZ (F. E.), WELCH (P. L.), GALTSOFF (P.-S.) & NEEDHAM (J. G.), 1937. — Culture methods for invertebrate animals. New York : Dover, 1959.

MARTIN (M. M.), 1979. — Biochemical implications of insect mycophagy. *Biol. Rev.*, **54**: 1-21.

MACDONALD (A.-J.), 1972. — Biology and behaviour of a mushroom infesting sciarid *Lycoriella mali* (Fitch). Ph. D. Thesis, Pennsylvania State University.

MADWAR (S.), 1937. — Biology and morphology of the immature stages of Mycetophilidae (Diptera : Nematocera). *Phil. Trans. R. Soc. London (B)*, **227**: 1-110.

MARTIN (M. M.), 1979. — Biochemical implications of insect mycophagy. *Biol. Rev.*, **54**: 1-21.

MINDERMAN (G.) & DANIELS (L.), 1967. — Colonisation of newly fallen laves by microorganisms. In : « Progress in Soil Biology », ed. Graff (O.) & Satchell (J. E.), *North-Holland* Publishing Co., Amsterdam, 3-9.

MOLITORIUS (H. P.), VANETTEN (J.-L.) & GOTTLIEB (D.), 1968. — Altersbedingte Anderungen der Zusammensetzung und des Stoffwechsels bei Pilzen. *Mushr. Sci.*, **7**: 59-67.

NEF (L.), 1957. — État actuel des connaissances sur le rôle des animaux dans la décomposition des littières de forêts. *Agricultura, Louvain*, **5**: 245-316.

OLECHOWICZ (E.), 1970. — Evaluation of number of insects emerging in meadow environment. *Bull. Acad. polon. Sci. Cl. II Sér. Sci., biol.*, **18**: 389-395.

PHERSON (D. A.), & BEATTIE (A. J.), 1979. — Fungal loads of invertebrates in beech litter. *Rev. Écol. Biol. Sol.*, **16**: 325-335.

POTTS (G. R.) & VICKERMAN (G. P.), 1974. — Studies on the cereal ecosystem. *Adv. Ecol. Res.*, **8**: 107-51.

POBOZSNY (M.), 1976. — *Bradysia brunnipes* (Meigen, 1804) (Diptera : Sciaridae) und ihr Bedeutung für die Streuzersetzung. *Acta zool. hung.*, **22**: 139-143.

PLACHTER (H.), 1979. — Zur Kenntnis der Präimaginalstadien der Pilzmücken (Diptera, Mycetophiloidea). II : Eidonomie der Larven. *Zool. Jb. Anat. Ontog. Tiere*, **101**: 271-392.

RAW (F.), 1967. — Arthropoda (except Acari and Collembola). Ch. 10, In : « Soil Biology », eds. Burges (A.) & Raw (F.), *Academic Press*, London, 323-362.

RUSSEL-SMITH (A.), 1979. — A study of fungus flies (Diptera : Mycetophilidae) in beech woodland. *Ecol. ent.*, **4**: 355-364.

SAITO (T.), 1966. — Sequential pattern of decomposition of beech litter with special reference to microbial succession. *Ecol. Rev. Sendai*, **16**: 245-254.

SAKHAROVA (A. V.), 1977. — The fungus gnats (Diptera : Mycetophilidae) of Moscow province. *Ent. Rev. Wash.*, **56**: 50-57.

SCHAERFFENBERG (B.), 1939. — Untersuchungen über die Coleopteren- und Dipterenfauna des Weidenbodens. *Z. angew. Ent.*, **26**: 536-544.

SOUTHWOOD (T. R. E.), MAY (R. M.), HASSELL (M. P.) & CONWAY (G. R.), 1974. — Ecological strategies and population parameters. *Am Nat.*, **108**: 791-804.

STEFFAN (W. A.), 1966. — A generic revision of the family Sciaridae (Diptera) of America, North of Mexico. *Univ. Calif. publ. Entomol.*, **44**: 1-77.

THIEDE (U.), 1977. — Untersuchungen über die Arthropoden fauna in Fichtenforsten. *Zool. Jb. Syst. Bd.*, **104**: 137-202.

TRIFOURKIS (S.), 1977. — The bionomics and taxonomy of the larval Mycetophilidae and other fungicolous Diptera. Ph. D. Thesis, University of London.

TUOMIKOSKI (R.), 1957. — Beobachtungen über einige Sciariden (Dipt.) deren larvae in faulem Holz oder unter der Rinde abgestorbener Baüme leben. *Ann. ent. fenn.*, **23**: 3-35.

TUOMIKOSKI (R.), 1960. — Zur Kenntnis der Sciariden (Dipt.) Finnlands. *Ann. Zool. Soc. 'Vanamo*, **21**: 1-164.

TWINN (D. C.), 1974. — Nematodes. In : « Biology of plant litter decomposition ». Eds. Dickinson (C. H.) & Pugh (G. J. F.). Vol. 2. *Academic Press*, New York, 421-465.

ZACHARIAE (G.), 1965. — Spuren tierischer Tatigkeit in Boden des Buchenwaldes. *Forstwiss. Forsch.*, **20**: 1-68.